Scientific paper

Redescription of the ocellus-bearing cuskeel *Neobythites kenyaensis* (Ophidiidae), with new Southeast African records and remarks on intraspecific morphological and colour variation

by

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Latitudinal trend
Quantitative otolith characters

Abstract. – *Neobythites kenyaensis*, a cuskeel (Ophidiidae) with two ocelli on the dorsal fin, is redescribed based on 33 meristic, body shape, colour, and otolith characters obtained from 15 specimens, 12 of which were studied for the first time. Nine of the 12 new specimens were collected during a research cruise off Mozambique together with vouchered colour photographs made on board when the fish were still fresh. Two specimens were collected off Natal, South Africa, one of them only available as a fresh colour photograph and one specimen off Dar es Salaam, Tanzania. Accordingly, while *N. kenyaensis* was only known from Kenya and northernmost Tanzania (Zanzibar) since its description in 1995, we proved now its continuous distribution along the entire SE African coast from off Ras Ngomeni, Kenya, to off Durban, South Africa, at depths of 238-457 m. *Neobythites kenyaensis* is rather unique among the 54 species of its genus in possessing an ocellus positioned near the dorsal-fin origin (anterior ocellus) which it shares only with the West-Pacific *N. longiventralis* and West-Atlantic *N. ocellatus*. It differs from the latter in the following characteristics: second, central ocellus more posteriorly placed on dorsal fin, more precaudal vertebrae (13 *vs.* 12), less developed gill rakers (8-10 *vs.* 14-16), shorter head (19.5-20.5 *vs.* 21.5-23.5% SL), and shorter pelvic fins (9.9-12.0 *vs.* 16.0-21.5% SL). Both species differ clearly from *N. longiventralis* in having a much shorter pelvin fin (9.9-21.5 vs. 32.0-34.% SL). The central ocellus-spot size, determined by the number of rays covered by the ocellus spot, varies considerably in *N. kenyaensis* and reaches the largest size reported for any ocellus-bearing *Neobythites* species. This character is strongly and positively correlated with both latitude and depth, suggesting gradual differentiation processes among adjacent populations or subpopulations. Another finding reported for the first time in Ophidiidae is the significant correlation of three otolith measurements with fish size (SL) in *N. kenyaensis*.

Résumé. – Redescription de *Neobythites kenyaensis* (Ophidiidae), incluant de nouvelles occurrences au Sud-Est de l'Afrique et des remarques sur les variations intraspécifiques de morphologie et couleur.

Neobythites kenyaensis (Ophidiidae), caractérisée par deux ocelles sur la nageoire dorsale, est redécrite sur la base de 33 caractères méristiques, de la forme et la couleur du corps et des caractères de l'otolithe observés sur 15 spécimens, dont 12 étudiés pour la première fois. Neuf de ces 12 nouveaux spécimens ont été collectés lors d'une mission au large du Mozambique et des photographies ont été réalisées à bord sur le matériel frais. Deux spécimens ont été collectés au large du Natal (Afrique du Sud) dont un a été photographié frais, et un spécimen a été collecté au large de Dar es Salaam (Tanzanie). Alors que depuis sa description en 1995, *N. kenyaensis* n'était connu qu'au Kenya et tout au nord de la Tanzanie, à Zanzibar, nous montrons ici qu'elle occupe une aire continue au large de la côte sud-est de l'Afrique depuis Ras Ngomeni (Kenya) à Durban (Afrique du Sud) à des profondeurs de 238 m à 457 m. Parmi les 54 espèces connues du genre, *N. kenyaensis* se distingue par la présence d'un ocelle tout à l'avant de la nageoire dorsale (ocelle antérieur), présent ailleurs seulement chez *N. ocellatus*, dont elle se distingue par les caractères suivants : le second ocelle, central, est en position plus postérieure sur la nageoire dorsale, un plus grand nombre de vertèbres précaudales (13 *vs.* 12), les branchies moins développées (8-10 *vs.* 14-16), une tête plus courte (19,5-20,5% SL *vs.* 21,5-23,5% SL), et des nageoires pelviennes plus courtes (9,9-12,0% SL *vs.* 16,0-21,5% SL). De plus, la taille de l'ocelle central, déterminée comme le nombre de rayons couverts, varie considérablement chez *N. kenyaensis* et atteint les plus grandes dimensions connues pour une espèce de *Neobythites*. Ce caractère est fortement et positivement corrélé à la latitude et la profondeur, suggérant une différenciation graduelle de populations adjacentes ou sous-populations. Pour la première fois chez les Ophidiidae, nous mettons en évidence une corrélation significative entre la taille des trois otolithes et celle du poisson (SL).

The cuskeel genus *Neobythites* is the most diverse genus among the family Ophidiidae with 54 valid species (Uiblein and Nielsen, 2018), which primarily occur on or close to the bottom of the deeper shelf and upper slope of tropical and subtropical zones of all major oceans. From the region of the Western Indian Ocean (WIO), 13 *Neobythites* species are known, of which six have one or two ocelli placed on the dorsal fin. These six ocellus-bearing species are

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N. crosnieri Nielsen, 1995, *N. gloriae* Uiblein & Nielsen, 2018, *N. kenyaensis* Nielsen, 1995, *N. malhaensis* Nielsen, 1995, *N. meteori* Nielsen, 1995, and *N. stefanovi* Nielsen & Uiblein, 1993.

Typical ocelli in *Neobythites* consist of a dark rounded spot surrounded by a concentric white ring (Uiblein and Nielsen, 2005). Four of the six WIO ocellus-bearing species have a single ocellus placed close to mid of body (termed "central" ocellus by Uiblein and Nielsen, 2005), while *N. crosnieri* and *N. kenyaensis* have two ocelli each. In *N. crosnieri* both ocelli are placed in the posterior region of the body (hence termed "posterior" ocelli). *Neobythites kenyaensis* has a central ocellus and one additional ocellus placed close to the origin of the dorsal fin ("anterior" ocellus). The specific placement of the two ocelli in *N. kenyaensis* is unique among Indian Ocean congeners and occurs only in *N. ocellatus* Günther, 1887 from the western Atlantic (Nielsen *et al*., 2009) and *N. longiventralis* Nielsen, 1997 from the West Pacific (Nielsen, 2002).

Neobythites kenyaensis was described based on two specimens collected off Kenya and northern Tanzania and only one more specimen from Kenya has been studied since the original description (Nielsen, 2002). During a cruise with the Norwegian R/V *Dr. Fridtjof Nansen* off Mozambique in October/November 2007 several *Neobythites* specimens were caught that were preliminarily identified as *N. kenyaensis* on board (Johnsen *et al.,* 2008). Closer inspection of those specimens and associated fresh colour photos taken shortly after their capture indicated slight deviations in ocellus characteristics from the types. In subsequent studies at the South African Institute for Aquatic Biodiversity (SAIAB) and the Zoological Museum of the University of Copenhagen (ZMUC), we included also two additional specimens, one from Tanzania and one from South Africa, and an unvouchered fresh photograph of a specimen collected off Natal, South Africa, all with a closely resembling ocellus pattern.

Based on these newly studied specimens and photographs of fresh fish, we provide a redescription and updated diagnosis of *N. kenyaensis* along with intra- and interspecific comparisons, considering meristic, body form, colour, and otolith characters. We update the distribution information of this species and report new records for the large area between Dar es Salaam, Tanzania, to Durban, South Africa. Furthermore, we use the new data set representing *N. kenyaensis* from a wide size and distributional range to search for intraspecific variation among morphological and colour characters and their relationships with size, geographic position and depth of occurrence. The results are discussed emphasizing the need of further comparative studies of morphological and colour diversity in association with species, population, and ecological differences in *Neobythites* and other Ophidiidae species.

MATERIAL AND METHODS

Of in total 14 *Neobythites kenyaensis* collected with bottom trawls by research or fishing vessels off the East African coast between Kenya and Natal, South Africa, standard length (SL) and counts or measurements of 12 meristic, 10 body shape, six ocellus and five otolith characters were obtained and compared. Fresh colour photographs of six vouchered specimens and one additional unvouchered specimen were also examined. Meristic characters, body-shape measurements, and qualitative morphological characters follow Nielsen *et al*. (1999) and Nielsen *et al*. (2009). Otolith measurements follow Uiblein *et al*. (2008) and description and analysis of colour patterns follow Uiblein and Nielsen (2005, 2018). Definitions of ocellus characters are given below. If not otherwise indicated, all morphometric data (body-shape and otolith measurements) are given as percentage of SL. Ranges of the resulting values below 10 were rounded to one decimal place and between 10 and below 50 to the nearest 0.5. The means of all measurements and counts were rounded to one decimal.

Morphometric and meristic ocellus characters for *N. kenyaensis* are termed and defined as follows: "anterior ocellus" is the ocellus placed close to the origin of the dorsal fin; "central ocellus" is the ocellus placed close to mid-body; "ocellus-spot distance" is the distance between upper-jaw symphysis and the anterior edge of the respective ocellus spot and provides a measurement of ocellus-spot position in relation to body; "number of ocellus-spot rays" is the number of dorsal-fin rays in (covered by) the respective ocellus spot and is a count referring to ocellus length and size; and "central-most ray in spot" is the dorsal-fin ray closest to the middle of the ocellus spot and indicates ocellus-spot position in relation to dorsal fin.

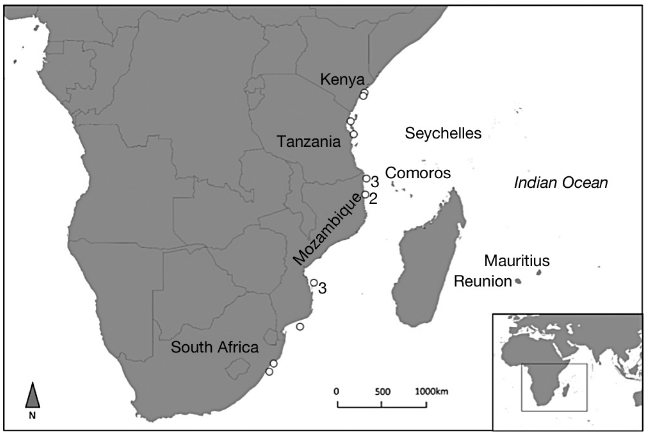

Figure 1. – Map with sampling localities for *Neobythites kenyaensis*. Number of specimens indicated for localities with multiple occurrences.

For comparisons with congeners, published data were used (*e.g*. Nielsen, 1995, 1999, 2002; Uiblein and Nielsen, 2005, 2018; Nielsen *et al.,* 2009). For detecting allometric relationships, all characters were plotted against SL. For detecting possible relationships with depth and geographic distribution, average depth and latitude were used. Because all occurrence data were north-south aligned along the East African coast (Kenya to South Africa; Fig. 1), latitude of collecting localities was a good proxy of geographic position. For statistical examination of the relationships between quantitative morphological and colour characters, fish size (SL), geographic position (latitude), and depth, linear regressions were calculated (GraphPad Prism version 5.00 for Windows, GraphPad Software, La Jolla California USA, www.graphpad.com). Two meristic characters, pectoral-fin ray number and dorsal-fin origin above vertebra number, did not pass the preceding normality test and hence were excluded from the analyses. Because of the low sample sizes (n = 10-15), significance level for the regression analyses was globally set to $p < 0.01$.

Institutional acronyms follow Fricke and Eschmeyer (2017); HT = holotype, PT = paratype.

RESULTS

Taxonomy

Neobythites kenyaensis Nielsen, 1995

(Figs 1-6; Tabs I, II)

Neobythites kenyaensis Nielsen, 1995: 5

Neobythites kenyaensis: Nielsen, 2002: 37

Holotype. – SAIAB (earlier RUSI) 13952, 124 mm SL, off Ras Ngomeni, Kenya, 2°50'S-40°31'E, R/V *Dr. Fridtjof Nansen*, 275 m depth.

Paratype. – BMNH 1939.5.24.1439, female, 103+ mm SL, off Zanzibar, Tanzania, 5°34'24"S-39°14'05"E; R/V *John Murray*, 238-293 m depth.

Other material (n = 13; 12 specimens and one unvouchered photograph; 97-162+ mm SL). – Kenya: USNM 340896, 140 mm SL; off Ras Ngomeni, 2°56'S-40°28'E, R/V *Anton Bruun*, 240 m depth; Tanzania: ZMA 113428, 148 mm SL, off Dar es Salaam, 274-457 m depth; Mozambique: SAIAB 82154, 3, 135-151 mm SL, 21°15'46"S-35°39'41"E, R/V *Dr. Fridtjof Nansen* (Station BT 70), 394-400 m depth; SAIAB 98890, two females, 97-102 mm SL, R/V *Dr. Fridtjof Nansen* (Station BT 135), 12°41'43"S-40°40'E, 292-296 m depth; SAIAB 98891, 3 females, 101-121 mm SL, 11°08'28"S-40°46'11"E, R/V *Dr. Fridtjof Nansen* (Station BT 136), 391-412 m depth; SAM F033865, female, 143 mm SL, 25°32'S-34°19'E, R/V *Algoa*, 372 m depth; South Africa: SAIAB 188287, 162+ mm SL, off Tugela Bank, 29°07.5'S-31°45.00'E, F/V *Ocean Spray*, 300-350 m depth; unvouchered photograph (Fig. 2D): SAIAB 95778, 148 mm SL, South Africa, Natal, off Durban, 29°54'54"S-31°19'46"E, F/V *Ocean Spray*, 427-435 m depth (photographer: Desmond Hayes).

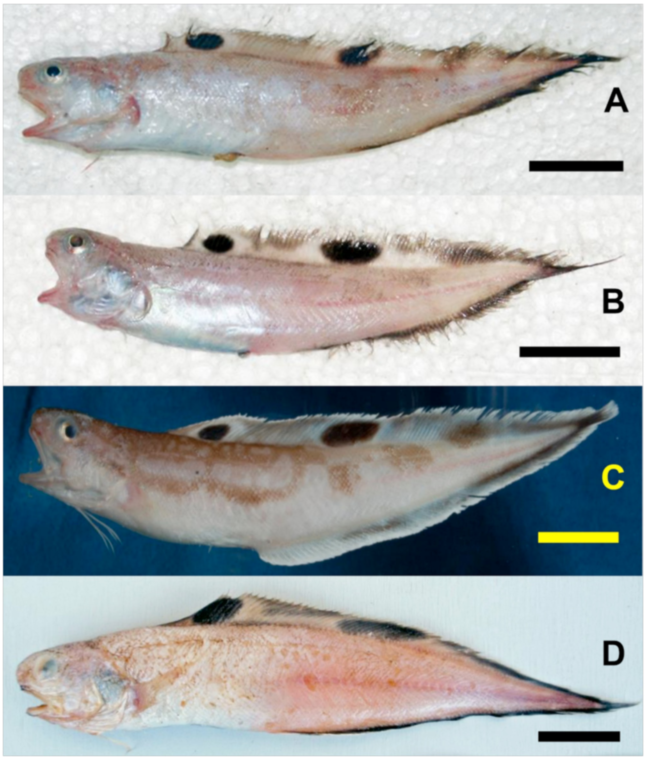

Figure 2. – Photographs of fresh specimens of *Neobythites kenyaensis*. **A**: SAIAB 98891, 121 mm SL, northern Mozambique (F. Uiblein); **B**: SAIAB 98891, 101 mm SL, northern Mozambique (F. Uiblein); **C**: SAIAB 82154, 136 mm SL, southern Mozambique (P.C. Heemstra); **D**: SAIAB 95778, 148 mm SL, off Durban, South Africa (D. Hayes). The horizontal size bars indicate 20 mm length.

Diagnosis

No spines on hind margin of preopercle; dorsal fin-rays 97-102; anal-fin rays 80-84; pectoral fin-rays 26-32; precaudal vertebrae 13; total vertebrae 55-59; pseudobranchial filaments 2-4; long gill rakers on anterior arch 8-10; head length 19.5-21.5% SL; pelvic-fin length 9.9-12.0% SL, pelvic fins reaching about halfway to anus; orbit length 4.3-5.3% SL, 22.0-30.5% head length, and 1.8-2.1 times in upper-jaw length; longest gill filament 1.4-2.3% SL and 6.9-12.0% head length; dorsal fin with two ocelli, the first one anterior of anus ("anterior ocellus") and the other ocellus centrally on body well behind anus ("central ocellus"); anterior ocellus spot distance 29.5-34.5% SL, the spot covering 6-9 dorsal-fin rays; central ocellus-spot distance 53-57% SL, the spot covering 8-15 dorsal-fin rays; caudal fin entirely and dorsal and anal fins at least in their posterior parts dark pigmented; otolith length 4.9-5.8% SL, sulcus length 3.4-4.7% SL, ostium height 20.0-24.0% sulcus length, and ostium height 28.5-37.5% ostium length.

Description (based on the two types, 12 additional specimens, and one unvouchered photograph)

Rather elongate fish with complete but mostly indistinct lateral line; head and body covered with cycloid scales; origin of dorsal fin above proximal part of pectoral fin; origin of anal fin in front of midpoint of fish; tip of pectoral fins ending well in front of anal fin; pelvic fins reaching almost halfway to origin of anal fin; length of blunt snout about diameter of eye; upper jaw ending well posterior to eye; anterior nostril ending in a short tube and larger posterior nostril with a low ridge; no spines on preopercle; strong opercular spine; anterior gill arch with 2-3 blunt and two long rakers on upper branch; one long raker in angle and lower branch with 5-7 long (total long gill rakers 8-10) and 5-7 blunt rakers; gill filaments 1.1-1.4 times as long as longest gill rakers; distinct pseudobranchial filaments 2-4 (2-3).

Otoliths (11 non-type specimens; Fig. 3)

Otolith oval, its height 1.4-1.6 times in its length; sulcus large, 1.2-1.5 times in otolith length; ostium 1.4-1.8 times in sulcus length; ostium height 2.7-3.5 times in ostium length.

Dentition

Premaxillaries and dentaries with granular teeth in many irregular rows. Vomer variably triangular shaped with many granular teeth. Palatines with several rows of granular teeth. Two median basibranchial tooth patches; the anterior elongate and the posterior much smaller and circular.

Axial skeleton (from radiographs; Fig. 4)

Precaudal vertebrae 13 and caudal vertebrae 42-46. All neural and haemal spines thin and pointed. First neural spine 1/3 in length of second spine, which is longer than the subsequent spines. Basis of neural spines enlarged. Parapophyses present on posterior 6-7 precaudal vertebrae. Pleural ribs on vertebrae 3-13. Epipleural ribs indistinct.

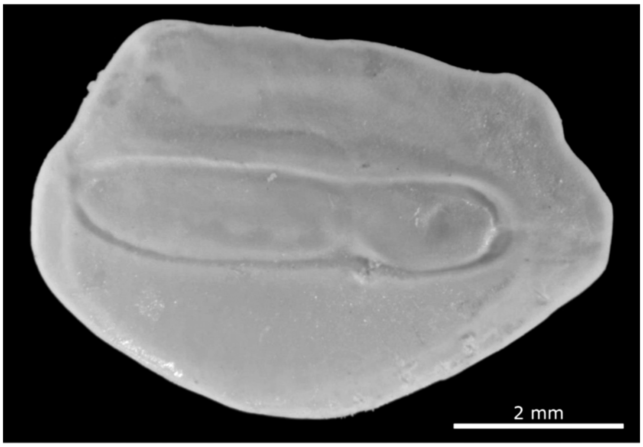

Figure 3. – Right otolith of *Neobythites kenyaensis*, SAIAB 98891, 121 mm SL (M. Krag).

Colour, fresh fish (Fig. 2)

Body and head pale brown or pale rose; head dorsally from snout level and anterior dorsal half of body sometimes with brown pigmentation alternating with pale-oval patches of different forms and sizes; posterior half of body mostly pale, sometimes anteriorly with two to three brown patches and/or further posteriorly with up to four weakly indicated vertical bars of about orbit width; abdomen whitish silvery to grey blue; lateral line mostly indistinct; dorsal fin in part pale-brown or brown pigmented with two ocelli composed of a black round spot surrounded by a white concentric ring and, more posterior, with a weaker indicated dark brown spot (visible in four of seven freshly photographed specimens); anterior ocellus nearly circular on erected fin, of about two to three times the size of orbit, placed above tip of pectoral fin or just behind it and well before anus; the second, central ocellus of at least three times the size of orbit and rather variable in size, more oval-formed (vertically flattened), and placed slightly behind mid body and well behind anus; the dark spot placed in posterior-most quarter of body, connecting posteriorly with the dark pigmentation of the dorsal fin forming a dark-brown fin margin that is distally accompanied by paler fin-ray tips; caudal fin dark-brown pigmented; anal fin in posterior-most third part or entirely dark-brown pigmented, with fin rays distally paler; pelvic and pectoral fins hyaline.

Colour, preserved fish

Body pale and head pale brown, pigmentation only partly retained or completely lost (pending also on preservation conditions and length); gill cavity brownish; abdomen and eyes bluish; lateral line indistinct; ocelli dark brown, remaining dorsal-fin pigmentation and pigmentation of caudal and anal fins mostly retained.

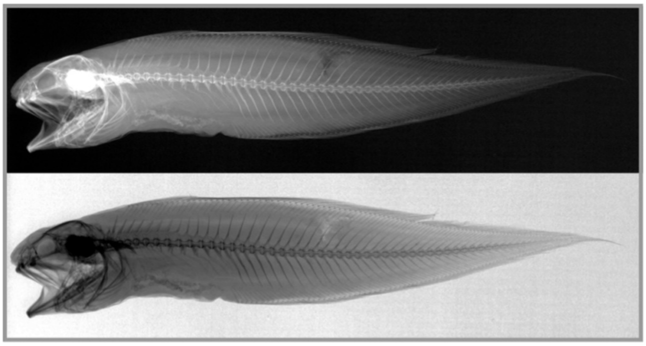

Figure 4. – Radiograph of *Neobythites kenyaensis*, SAIAB 98890, 102 mm SL (M. Lisher). Inverted colour version on bottom.

Table I. – *Neobythites kenyaensis* quantitative morphological and colour characters. + Tail anterior to caudal-fin base broken and missing.

	Kenya		Tanzania		Mozambique				South Africa		all			
	HT	USNM	PT	ZMA	Min	Mean	Max	n	SAIAB	Photo	Min	Mean	Max	n
Standard length (SL, in mm)	124+	140	103+	148	97	121	151	9	162+	148	97	127.6	162	15
Meristic characters														
Dorsal-fin rays	102	98		98	97	98.4	100	9	100		97	98.8	102	13
Caudal-fin rays		8		8	7	7.6	8	8			7	7.7	8	10
Anal fin-rays		83		84	80	81.3	83	9	82		80	81.8	84	12
Pectoral-fin rays	29	29	29	29	26	28.1	32	9	28		26	28.4	32	14
Precaudal vertebrae	13	13	13	13	13	13	13	9	13		13	13	13	14
Total vertebrae	56	58		59	55	56.9	58	9	59		55	57.1	59	13
Pseudobranchial filaments	3	2	2	3	2	3	4	6	3		2	2.8	4	11
Dorsal-fin origin above vertebra no.	4	5	5	5	4	4.4	5	9	4		4	4.5	5	14
Anal-fin origin below dorsal-fin ray no.	22	21	20	20	20	21.6	22	9	22		20	21.4	22	14
Anal-fin origin below vertebra no.	16	15	15	15	14	15.3	16	9	16		14	15.4	16	14
Developed gill rakers	9	10	9	9	8	9.1	10	9	9		8	9.1	10	14
Total gill rakers		18		18	16	17.6	19	7	18		16	17.7	19	10
Morphometric characters (in% SL)														
Body depth at anal-fin origin	19.0	18.5	19.0	18.0	16.5	18.1	19.5	9	18.0		16.5	18.2	19.5	14
Head length (HL)	20.5	20.0	21.5	20.0	19.5	20.1	20.5	9	20.0		19.5	20.2	21.5	14
Postorbital distance	12.0	11.5	12.0	12.0	11.0	11.7	13.0	9	12.0		11.0	11.8	13.0	14
Orbit length	5.2	4.8	5.1	4.9	4.3	5.0	5.3	7	5		4.3	5.0	5.3	12
Upper-jaw length	9.6	9.6	9.7	10.5	9.1	9.7	10.0	9	9.6		9.1	9.7	10.5	14
Preanal distance	43.5	44.5	44.0	40.0	37.5	40.2	42.5	9	37.0		37.0	40.8	44.5	14
Predorsal distance	24.0	24.0	26.5	25.5	22.0	23.7	26.0	9	24.5		22.0	24.2	26.5	14
Pelvic-fin to anal-fin origin distance	29.0	26.0		28.0	24.5	26.6	28.5	9	24.0		24.0	26.7	29.0	13
Pelvic-fin length	12.0	10.5		10.5	9.9	10.7	12.0	9	12.0		9.9	10.8	12.0	13
Gill-filament length	1.7	1.4	1.5	2.0	1.5	1.87	2.4	9	1.5		1.4	1.8	2.3	14
Anterior ocellus-spot distance	34.5	31.5	32.0	31.5	29.5	31.3	33.5	9	31.5		29.5	31.6	34.5	14
Central ocellus-spot distance	56	55	55	56	53	54.2	57	9	53		53	54.5	57	14
Morphometric characters (in% HL)														
Postorbital distance	58	57	58	60	56	58.5	64	9	59		56	58.5	64	14
Orbit length	25.5	24.0	24.5	24.5	22.0	26	30.5	7	25.0		22.0	25.6	30.5	12
Upper-jaw length	46.0	48.5	46.5	52	45.0	48.3	51	9	48.0		45.0	48.4	52	14
Gill-filament length	8.3	6.9	7.4	10.0	7.8	9.3	12.0	9	7.7		6.9	8.9	12.0	14
Orbit length in% upper-jaw length	54	49.5	53	47.0	47.5	51.0	54	7	52		47.0	51.0	54	12
Ocellus meristic characters														
Anterior ocellus														
Number of ocellus-spot rays	7	8	6	8	6	7.7	9	9	9	9	6	7.7	9	15
Central-most ray in spot	17	16	15	11	13	14	15	9	14		11	14.21	17	14
Central ocellus														
Number of ocellus-spot rays	8	9	9	12	11	12.2	14	9	12	15	8	11.7	15	15
Central-most ray in spot	40	40	39	40	39	40.6	43	9	40		39	40.3	43	14
Otolith characters (in% SL)														
Otolith length		5.5		5.5	4.9	5.1	5.8	8	5.6		4.9	5.2	5.8	11
Otolith height		3.8		3.6	3.1	3.4	3.8	8	3.6		3.1	3.5	3.8	11
Sulcus length		4.1		4.0	3.4	3.7	4.7	8	4.5		3.4	3.8	4.7	11
Ostium length		2.6		2.6	2.1	2.4	2.6	8	2.9		2.1	2.5	2.9	11
Ostium height		0.9		0.9	0.7	0.8	1.0	8	1.1		0.7	0.8	1.1	11
Ostium height in% Sulcus length		22.0		22.5	20.0	21.8	24.0	8	24.0		20.0	21.8	24.0	11
Ostium height in% Ostium length		34.5		34.0	28.5	33.2	37.0	8	37.5		28.5	33.8	37.5	11

Distribution and size (Fig. 1)

SW Indian Ocean: from Kenya, off Ras Ngomeni, to Tanzania, Mozambique, and off Durban, Natal (South Africa); new for the entire area off Southeast Africa from south of Zanzibar to Natal; 238-457 m depth; maximum size at least 162 mm SL.

Comparisons

Intraspecific comparisons

Neobythites kenyaensis shows considerable intraspecific variation in the number of rays covered by the central ocellus spot. While 8 or 9 rays are covered in the three specimens (including the types) from Kenya and northernmost Tanzania, all other specimens from further south have 11 to 15 rays covered by the spot. Compared to the central-ocellus spot, the anterior ocellus spot is mostly smaller and does become only slightly larger southwards, from 6-8 covered rays north of Dar es Salaam to 6-9 covered rays in Mozambique and 9 covered in South Africa. Consequently, the size difference between the two ocellus spots increases southwards from one to six additional dorsal-fin rays covered by the central ocellus spot. Regarding otoliths, the slightly larger relative ostium length and ostium height in the South African specimen may reflect a size trend rather than a geographic difference (see also Remarks section).

Interspecific comparisons

Among the entire genus similar colour characteristics are only shared by the Western Atlantic *N. ocellatus*, and the West-Pacific *N. longiventralis*. The latter differs however clearly from the two other species in a much longer pelvic fin (32-34.5 *vs*. 9.9-21.5% SL) (Nielsen, 2002; Nielsen *et al*., 2009). In the more similar *N. ocellatus*, the central ocellus spot is, however, placed further anteriorly (central ocellus-spot distance 45.0-50 *vs*. 53-57% SL in *N. kenyaensis*). Both species overlap in anterior ocellus-spot distance (28.0-30.0% SL in *N. ocellatus vs*. 29.5-34.5% SL), number of rays covered by the ocellus spots (anterior ocellus, 6-9 rays in *N. kenyaensis vs*. 5-7 rays in *N. ocellatus*; central ocellus, 8-15 *vs*. 8-11 rays), and facultative occurrence of a dark spot placed on the posterior part of the dorsal fin.

By non-colour characteristics *Neobythites kenyaensis* can be distinguished from *N. ocellatus* in having more precaudal vertebrae (13 *vs*. 12), less developed gill rakers (8-10 *vs*. 14-16), a shorter head (19.5-20.5 *vs*. 21.5-23.5% SL), and shorter pelvic fins (9.9-12.0 *vs*. 16.0-21.5% SL).

In all other 51 *Neobythites* species, no anterior ocellus occurs. In five species, *N. australiensis* Nielsen, 2002, *N. braziliensis* Nielsen, 1999, *N. marquesaensis* Nielsen, 2002, *N. multiocellatus* Nielsen, Uiblein & Mincarone, 2009, and *N. natalensis* Nielsen, 1995, a small dark spot occurs in place of the anterior ocellus, which is however not surrounded by a concentric white ring. In some specimens of *N. australiensis* the anterior dark blotch is completely absent (Nielsen, 2002).

Remarks

Each of the three examined variables, size (SL), geographic position (latitude), and depth, correlates significantly with one or several characters (Tab. II, Figs 5, 6). Strong positive correlations with fish size occurred in three otolith characters, sulcus length, ostium length, and ostium height, when expressed in% SL. Strong positive correlations with geographic position and depth occurred in central-ocellus size (= number of dorsal-fin rays in central-ocellus spot).

DISCUSSION

Neobythites kenyaensis shows a wide, rather continuous horizontal and vertical distribution along the East African coast from off Ras Ngomeni, Kenya, to off Durban, South Africa. The studied characters, while revealing some variability, do not indicate any divergence, singly or in combination, that would indicate to the existence of separate taxa. The strong correlation between central ocellus size and the distributional variables latitude and depth points to a gradual, still ongoing differentiation process among adjacent populations or subpopulations, *i.e*. a cline (Endler, 1977).

The dorsal-fin ocelli in *Neobythites* may have one or even several ecological functions. These eye-resembling structures may contribute to deter visually hunting predators or serve to deflect their attacks to less vital parts of the body, or they may assist in social communication and species recognition (Uiblein and Nielsen, 2005; see also Uiblein and Nielsen, 2018). The here observed geographic and/or bathymetric cline in ocellus size may reflect ongoing adaptive, evolutionary differentiation processes. More detailed insights into these processes could be gained by expanding this study to include more specimens from various areas and depth zones within the species' entire distribution range,

Table II. – Five quantitative characters, of which four were found to be significantly correlated with SL, latitude or depth, with results from linear regression analysis (significant data in bold). R^2: Linear regression coefficient; *: $p < 0.01$; **: $p < 0.001$; ns: not significant.

	SL		Latitude		Depth	
	R^2	Probability	R^2	Probability	R^2	Probability
Central ocellus-spot ray number	0.12	0.20^{ns}	**0.61**	**0.0005****	**0.55**	**0.002***
Sulcus length in% SL	**0.59**	**0.006***	0.12	0.30^{ns}	0.002	0.90^{ns}
Ostium length in% SL	**0.79**	**0.0003****	0.17	0.21^{ns}	0.001	0.92^{ns}
Ostium height in% SL	**0.75**	**0.0006****	0.26	0.11^{ns}	0.02	0.70^{ns}
Ostium height in% Sulcus length	0.19	0.17^{ns}	0.19	0.18^{ns}	0.03	0.64^{ns}

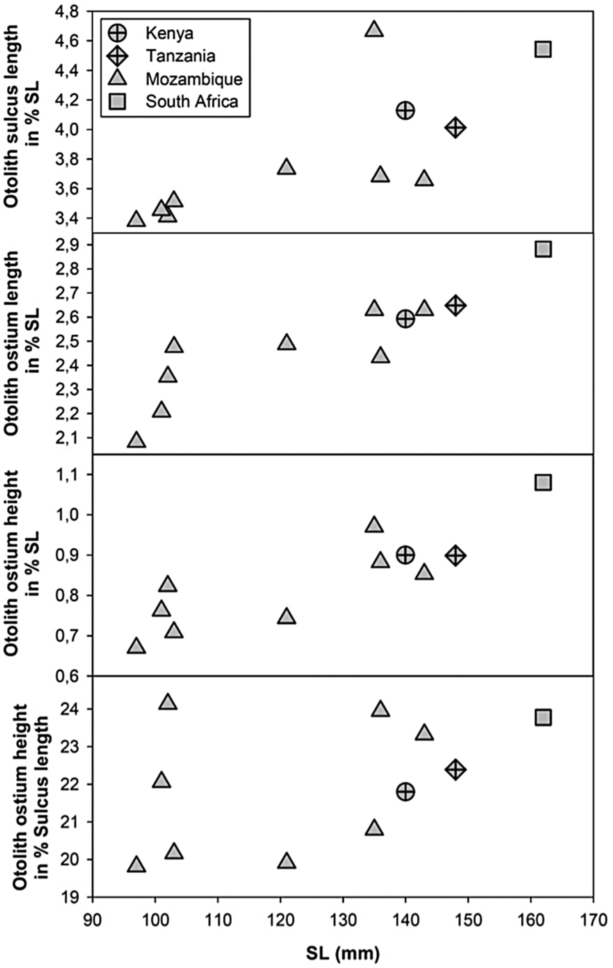

Figure 5. – Quantitative otolith characters in *Neobythites kenyaensis* plotted against SL.

in combination with ecological variables and support from genetics.

Three otolith characters showed allometry when expressed in% SL (Fig. 5). However, when expressed in relation to each other (*e.g.* ostium height in% sulcus or ostium length) the correlation with SL was very weak (Tab. I) indicating no allometry, as also evident from plotting against SL (Fig. 5). The occurrence of allometry in otolith quantitative characters of Ophidiidae is here reported for the first time. It will be important to consider these results in future studies as otolith characters often have diagnostic value. In the giant cuskeel genus *Spectrunculus*, for instance, otolith characters have been used to support the distinction between the sister species *S. crassus* (Vaillant, 1888) and *S. grandis* (Günther, 1877) (Uiblein *et al.,* 2008). Accordingly, the two *Spectrunculus* species could be well distinguished in relative ostium height. No indications for allometric variation in quantitative otolith characters were found. However, the otoliths studied by Uiblein *et al.* (2008) were from specimens within restricted size ranges and no small-sized *S. grandis* were considered. A follow-up study is currently underway involving specimens of *S. crassus* and *S. grandis* from wider size ranges.

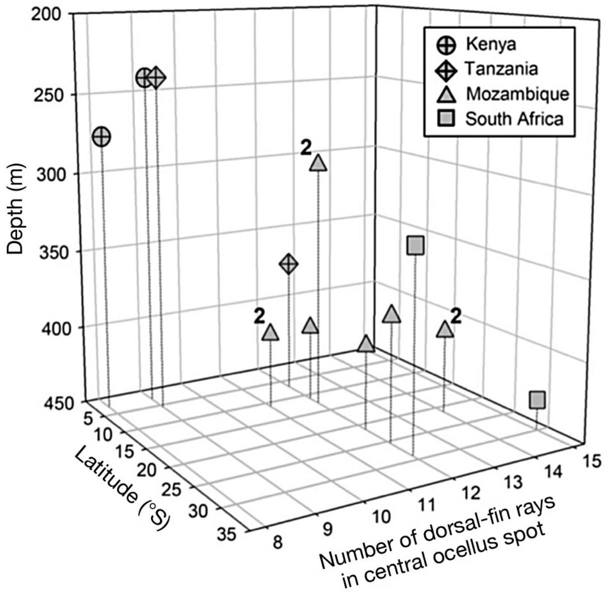

Figure 6. – Number of dorsal-fin rays in central ocellus spot plotted against latitude and depth in *Neobythites kenyaensis*. Numbers near symbols indicate multiple numbers of specimens referred to; with reference lines for each symbol.

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REFERENCES

ENDLER J., 1977. – Geographic Variation, Speciation, and Clines. 246 p. Princeton, N.J.: Princeton University Press.

FRICKE R. & ESCHMEYER W.N., 2017. – Guide to Fish Collections. Available from: http://researcharchive.calacademy.org/research/ichthyology/catalog/collections.asp (accessed 01 Feb. 2018).

JOHNSEN E., KRAKSTAD J.O., OSTROWSKI M., SERIGSTAD B., STRØMME T., ALVHEIM O., OLSEN M., ZAERA D., ANDRÉ E.R., DIAS N., SOUSA L., SOUSA B., MALAUENE B. & ABDULA S., 2008. – Surveys of the Living Marine Resources of Mozambique. Ecosystem Survey and Special Studies, 27 Sep.-21 Dec. 2007. 111 pages. Institute of Marine Research Bergen: Cruise reports “Dr. Fridtjof Nansen”.

NIELSEN J.G., 1995. – A review of the species of the genus *Neobythites* (Pisces, Ophidiidae) from the western Indian Ocean with description of seven new species. *Ichthyol. Bull.*, 62: 1-19.

NIELSEN J.G., 1999. – A review of the genus *Neobythites* (Teleostei, Ophidiidae) in the Atlantic, with three new species. *Bull. Mar. Science*, 65(2): 335-372.

NIELSEN J.G., 2002. – Revision of the Indo-Pacific species of *Neobythites* (Teleostei, Ophidiidae) with 15 new species. *Galathea Report*, 19: 5-105.

NIELSEN J.G., COHEN D.M., MARKLE D.F. & ROBINS R.C., 1999. – FAO species catalogue. Ophidiiform fishes of the world (Order: Ophidiiformes). Rome: FAO Fisheries Synopses, 125(18): 1-178.

NIELSEN J.G., UIBLEIN F. & MINCARONE M.M., 2009. – Ocellus-bearing *Neobythites* species (Teleostei: Ophidiidae) from the West Atlantic with description of a new species. *Zootaxa*, 2228: 57-68.

UIBLEIN F. & NIELSEN J.G., 2005. – Ocellus variation and possible functions in the genus *Neobythites* (Teleostei: Ophidiidae). *Ichthyol. Res.*, 52: 364-372.

UIBLEIN F. & NIELSEN J.G., 2018. – Review of the *steatiticus*-species group of the cuskeel genus *Neobythites* (Ophidiidae) from the Indo-Pacific, with description of two new species. *Zootaxa*, 4387: 157-173.

UIBLEIN F., NIELSEN J.G. & MØLLER P.R., 2008. – Systematics of the ophidiid genus *Spectrunculus* (Teleostei: Ophidiiformes) with resurrection of *S. crassus*. *Copeia* 2008(3): 542-551.